RESEARCH ARTICLE

Review of tapeworms of rodents in the Republic of Buryatia, with emphasis on anoplocephalid cestodes

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Abstract

Examination of ca. 500 rodents [*Microtus* spp., *Myodes* spp., *Cricetulus barabensis* (Pallas), *Apodemus peninsulae* Thomas] from 14 localities in the Republic of Buryatia (Russian Federation) revealed a minimum of 11 cestode species representing *Anoplocephaloides* Baer, 1923 *s. str.* (1 species), *Paranoplocephala* Lühe, 1910 *s.l.* (5 species), *Catenotaenia* Janicki, 1904 (2 species), *Arostrilepis* Mas-Coma & Tenora, 1997 (at least 2 species) and *Rodentolepis* Spasskii, 1954 (1 species). At least 5 of these species are previously unknown from the region. The taxonomic and phylogenetic position of Buryatian *Paranoplocephala* species was defined by cytochrome oxidase I (COI) sequences (mtDNA). The phylogenetic analysis also confirmed the status of *Parandrya* Gulyaev & Chechulin, 1996 as a junior synonym of *Paranoplocephala s.l.* The species diversity of anoplocephalid cestodes was significantly lower in Buryatia and North-East Siberia (6-7 species) than in Europe (17 species). The connections of the anoplocephalid fauna of Buryatia seem to be closer with Beringia (North-East Siberia and Alaska) than with Europe. The present study demonstrated high spatial variation (patchiness) among study sites in cestodes of Buryatian rodents, with the exception of the ubiquitous *Arostrilepis horrida* (von Linstow, 1901)-complex.

Keywords

Cestoda, Anoplocephalidae, Catenotaeniidae, Hymenolepididae, *Paranoplocephala*, voles, Buryatia
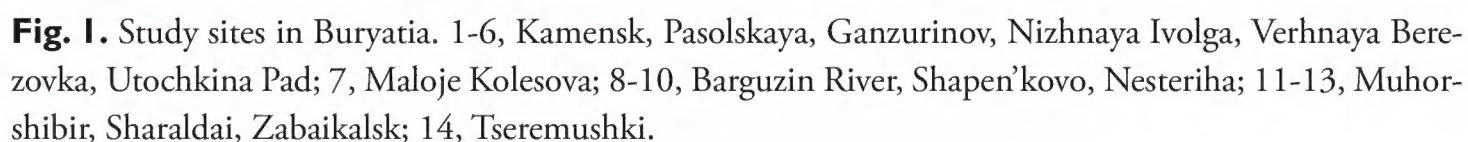
Introduction

The rodent fauna of the Republic of Buryatia (Russian Federation) represents a mixture of Asian, northern Palaearctic and Holarctic species. Of the Buryatian rodents, the grey-sided vole *Myodes rufocanus* (Sundevall) (syn. *Clethrionomys rufocanus*), the red vole *Myodes rutilus* (Pallas) (syn. *Clethrionomys rutilus*) and the root vole *Microtus oeconomus* (Pallas) are distributed throughout northern Eurasia, the latter two extending into north-western North America. More southern Palaearctic elements include the reed vole *Microtus fortis* Büchner, Maximowicz's vole *Microtus maximowiczii* (Schrenk), the striped dwarf hamster *Cricetulus barabensis* (Pallas) and the Korean field mouse *Apodemus peninsulae* Thomas. Biogeographically the location of Buryatia is interesting because the east-west taiga corridor between the Lake Baikal and Mongolian steppe has probably been a major migration pathway for the Palaearctic fauna and flora (de Lattin 1967; Mikkola 1988).

The helminths of rodents in the Lake Baikal basin, including Buryatia, have been the subject of two major faunistical studies, i.e. those of Machul'skii (1958) and Zhaltsanova (1992). In addition, four recent descriptions of new species of anoplocephalid cestodes have included material from Buryatia (Chechulin and Gulyaev 1998; Gulyaev and Chechulin 1996; Gulyaev and Krivopalov 2003; Haukisalmi et al. 2007a). In terms of species diversity, anoplocephalid cestodes are the dominant helminth group in arvicoline rodents in Buryatia and elsewhere. However, some of the anoplocephalid cestodes previously reported from Buryatian rodents [i.e. *Paranoplocephala macrocephala* (Douthitt, 1915) and *P. microti* (Hansen, 1947)] are now known to be restricted to the Nearctic region (Haukisalmi and Henttonen 2003; Haukisalmi et al. 2004). Moreover, the apparently widespread *Paranoplocephala omphalodes* (Hermann, 1783) has been shown to include multiple species (Haukisalmi et al. 2004), and it is not known which of these species occur in Buryatia. Similar taxonomical problems are present in catenotaeniid cestodes. For example, *Catenotaenia pusilla* (Goeze, 1782) probably does not occur in *Microtus* Schrank and *Apodemus* Kaup in Buryatia, because it is presently regarded as a specific parasite of *Mus musculus* (L.) (Tenora and Murai 1975).

The present study reviews the cestode fauna of Buryatian rodents based on new extensive collections and includes recent advances in the taxonomy of anoplocephalid cestodes. The Buryatian cestode fauna of rodents is compared with those of Europe and north-eastern Siberia. Mitochondrial DNA sequences are used for defining the taxonomic and phylogenetic position of the *Paranoplocephala* species of Buryatian voles.

Material and methods

Rodents were trapped at 14 study sites of Buryatia in August in 2004 and 2005. The location of Buryatia, study sites therein, and the rodent material sampled from each locality are given in Fig. 1 and Table 1.

Fig. 1. Study sites in Buryatia. 1-6, Kamensk, Pasolskaya, Ganzurinov, Nizhnaya Ivolga, Verhnaya Berezovka, Utochkina Pad; 7, Maloje Kolesova; 8-10, Barguzin River, Shapen'kovo, Nesteriha; 11-13, Muhorshibir, Sharaldai, Zabaikalsk; 14, Tseremushki.

Table 1. Prevalence (%) of cestodes in various host species and study sites in Buryatia (if $N \geq 10$). If $N < 10$, presence has been shown by "+". Cestode species are: *Anoplocephaloides* cf. *dentata* (*Aden*), *Paranoplocephala* cf. *omphalodes* (*Pomp*), *P. blanchardi* (*Pbla*), *P. feodorovi* (*Pfeo*), *P. buryatiensis* (*Pbur*), *P. longivaginata* (*Plon*), *Catenotaenia* sp. 1 (*Cat1*), *Catenotaenia* sp. 2 (*Cat2*), *Arostrilepis horrida s.l.* (*Ahor*) and *Rodentolepis* sp. (*Rod*).

Host species Locality	Aden	Pomp	Pbla	Pfeo	Pbur	Plon	Cat1	Cat2	Ahor	Rod
***Apodemus peninsulae* (n=51)**								2		
Kamensk (n=8)								+		
Verhnaya Berezovka (n=8)										
Utochkina Pad (n=9)										
Barguzin River (n=8)										
Shapen'kovo (n=7)										
Muhorshibir (n=11)										
***Cricetulus barabensis* (n=83)**							6		1	24
Ganzurinov (n=22)							5			14
Nizhnaya Ivolga (n=1)										
Shapen'kovo (n=4)									+	

Host species / Locality	Aden	Pomp	Pbla	Pfeo	Pbur	Plon	Cat1	Cat2	Ahor	Rod
Muhorshibir (n=4)										
Sharaldai (n=49)							8			33
Zabaikalsk (n=3)										+
Myodes rufocanus (n=132)	**2**				**14**				**22**	
Kamensk (n=7)					+				+	
Pasolskaya (n=35)	6				43				6	
Maloje Kolesova (n=1)										
Verhnaya Berezovka (n=6)	+								+	
Utochkina Pad (n=10)					10				20	
Shapen'kovo (n=8)									+	
Muhorshibir (n=44)					3				30	
Tseremushki (n=21)									33	
Myodes rutilus (n=56)						**11**			**30**	
Pasolskaya (n=6)						+				
Maloje Kolesova (n=9)										
Verhnaya Berezovka (n=3)						+			+	
Utochkina Pad (n=1)						+				
Shapen'kovo (n=21)									52	
Muhorshibir (n=19)						5			42	
Tseremushki (n=7)						+				
Microtus fortis (n=129)	**3**	**12**	**2**	**1**	**2**				**29**	
Kamensk (n=24)		13			4				50	
Pasolskaya (n=2)									+	
Maloje Kolesova (n=12)		25	17	8					17	
Barguzin River (n=30)		20								
Shapen'kovo (n=25)	4								60	
Nesteriha (n=13)	23								23	
Muhorshibir (n=16)		6			13				6	
Zabaikalsk (n=7)		+							+	
Microtus oeconomus (n=26)		**12**							**27**	
Ganzurinov (n=8)		+								
Nizhnaya Ivolga (n=9)		+							+	
Utochkina Pad (n=1)										
Shapen'kovo (n=5)									+	
Tseremushki (n=3)										

We used snap-traps (Finnish metal mouse trap), which were set in the late afternoon and evening, and checked early next morning. In the field, rodents were placed in a Styrofoam box with coolers, kept in a refrigerator in a laboratory, and dissected the same day. The cestodes found were first allowed to relax in tap water, then fixed flat (without pressure) in 70% ethanol, and those used for morphology stained later with Mayer's haemalum, Semichon's acetocarmine or ironacetocarmine, cleared in eugenol and mounted in Canada balsam. Voucher specimens (whole-mounts) of all identified

cestode species from Buryatia have been deposited in the Museum of Southwestern Biology, University of New Mexico, USA (MSB) and the United States National Parasite Collection, Maryland, USA (USNPC).

Most of the comparative cestode materials from Chukotka, North-East Siberia, were collected in connection with the Beringian Coevolution Project (BCP; see Cook et al. 2005; Hoberg et al. 2003).

Seven specimens of *Paranoplocephala* Lühe, 1910 from Buryatia were sequenced for the partial cytochrome oxidase I (COI) gene and embedded in a larger COI sequence data set of *Paranoplocephala* spp., originating primarily from Wickström et al. (2005). GenBank numbers for the COI sequences are given in Fig. 2. For the extraction, amplification and sequencing of DNA, see Wickström et al. (2003, 2005) and Haukisalmi et al. (2004).

Altogether 43 COI sequences (569-679 bp) of *Paranoplocephala* spp. were aligned using Clustal X (Thompson et al. 1997) with sequences of *Andrya rhopalocephala* (Riehm, 1881) and *Neandrya cuniculi* (Blanchard, 1891), the latter two species from lagomorphs used as an outgroup. A neighbour-joining distance phylogram was constructed in PAUP* (version 4.0 b10; Swofford 2002) using Kimura 2-parameter distances. Bootstrap support for the topology was estimated through 10 000 pseudoreplicates.

Results

Anoplocephalidae

Anoplocephaloides cf. *dentata* (Galli-Valerio, 1905)

The names *Paranoplocephala dentata* (Galli-Valerio, 1905), *Anoplocephaloides dentata* (Galli-Valerio, 1905) and *Paranoplocephala brevis* Kirshenblat, 1938 have been variously used for small, wedge-shaped cestodes parasitizing voles of the genera *Microtus* and *Chionomys* Miller (and occasionally other hosts) in the Palaearctic region. The position of *A. dentata* within the genus *Anoplocephaloides* Baer, 1923, as suggested by Rausch (1976), has been generally accepted. Following Spasskii (1951), *P. brevis* has been consistently regarded as a junior synonym of *A. dentata*. Thus, all *A. dentata*-like cestodes in the Palaearctic voles have been considered a single species, with the exception of *Anoplocephaloides dentatoides* Sato, Kamiya, Tenora & Kamiya, 1993 from *Myodes rufocanus* from Hokkaido, Japan (see Sato et al. 1993).

A recent molecular phylogenetic analysis (Haukisalmi et al. 2009) suggested that *A. dentata*-like cestodes include at least five species (plus *A. dentatoides*) in the Holarctic region: four species in western Eurasia and one in the rest of Eurasia and Beringia (north-eastern Siberia and Alaska). Based on the cytochrome oxidase I (mtDNA) sequences, the *A. dentata*-like cestodes from Buryatia (hosts *Myodes rufocanus* and *Microtus fortis*) group strongly, and are therefore conspecific, with the Holarctic species
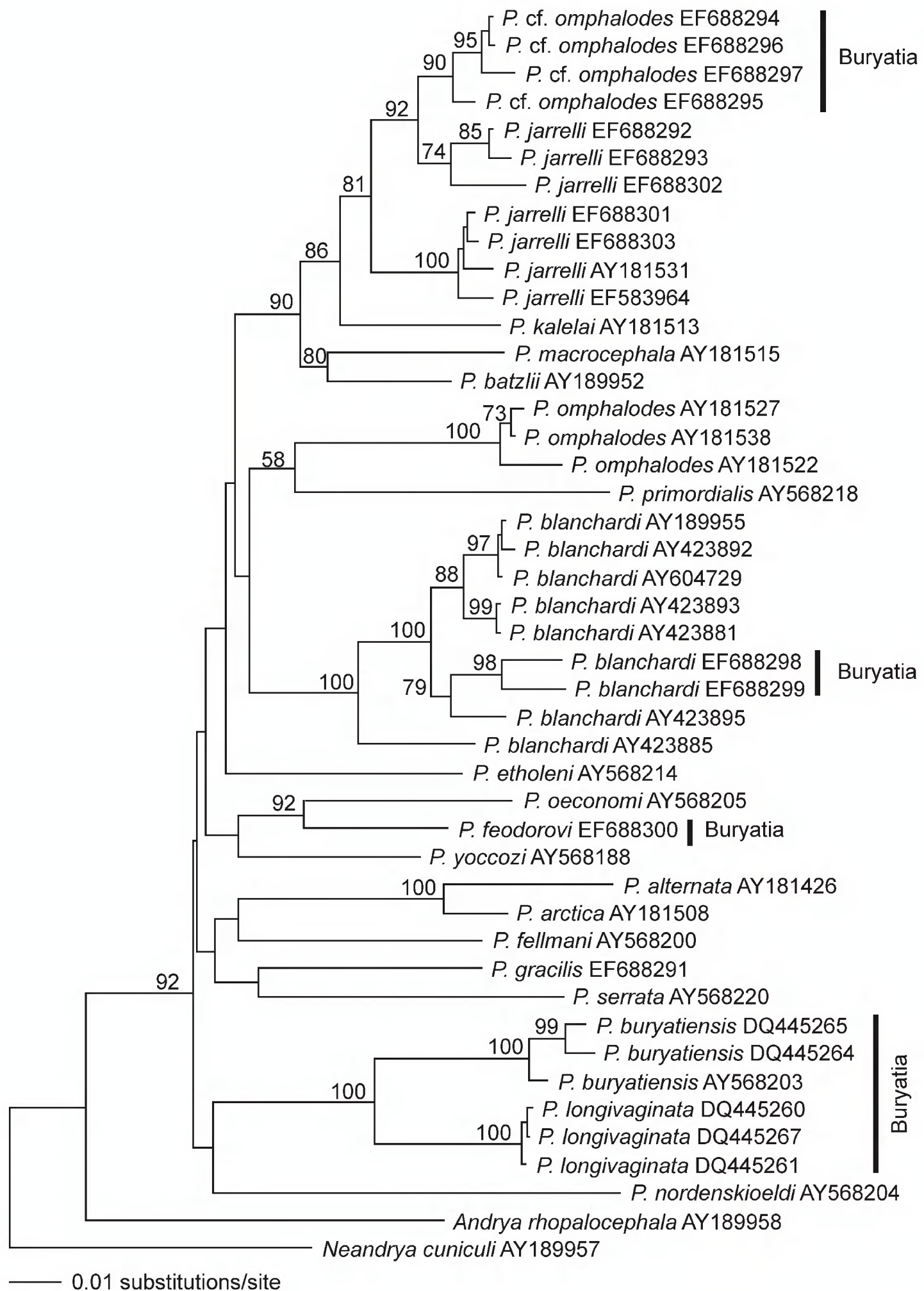
Fig. 2. A neighbour-joining reconstruction of partial cytochrome oxidase I (mtDNA) sequences of *Paranoplocephala* spp., *Andrya rhopalocephala* and *Neandrya cuniculi* from lagomorphs were used as an outgroup. The labels show the GenBank number for each sequence. Values at nodes show the percentage from 10000 bootstrap replicates.

(Haukisalmi et al. 2009). However, it is not yet known if this Holarctic species is conspecific with either of the two related species described in North America, i.e. *Anoplocephaloides infrequens* (Douthitt, 1915) and *A. troeschi* (Rausch, 1946) from *Geomys bursarius* (Shaw) (Geomyidae) and *Microtus pennsylvanicus* (Ord), respectively.

In the Palaearctic, *A. dentata*-like cestodes are characteristically parasites of voles of the genera *Microtus* and *Chionomys*. However, in addition to *Microtus gregalis* (Pallas), *M. maximowiczii* and *M. oeconomus*, Machul'skii (1958) and Zhaltsanova (1992) reported *P. brevis* or *P. dentata* from *Myodes rufocanus*, *M. rutilus*, *Apodemus peninsulae* and *Cricetulus barabensis* in Buryatia. In the present study, *A.* cf. *dentata* was found from *Microtus fortis* and *Myodes rufocanus*. It is probable that all *A. dentata*-like cestodes in Buryatia represent a single species, with the occurrences in *Myodes*, *Apodemus* and *Cricetulus* being accidental.

Because there are few morphological features useful for the diagnosis of *A. dentata*-like cestodes, sequence data (COI, 28S rRNA) have proved to be necessary tools in the taxonomy of this species complex (Haukisalmi et al. 2009).

Anoplocephaloides cf. *dentata* was significantly more prevalent in Nesteriha (23%) than in the other study sites (0-6%) (Table 1).

Voucher specimen: MSB Endo 152 from *Microtus fortis* (Nesteriha).

Paranoplocephala cf. *omphalodes* (Hermann, 1783)

It has been recently shown that *P. omphalodes sensu stricto* is primarily a parasite of *Microtus agrestis* (L.) and *M. arvalis* (Pallas) in Europe and probably elsewhere in western Eurasia (Haukisalmi et al. 2004). There is another, rather host-specific species in *M. oeconomus* (i.e. *Paranoplocephala jarrelli* Haukisalmi, Henttonen & Hardman, 2006) that occurs in the root/tundra vole throughout its Holarctic range. The *P. omphalodes*-like taxon occurring in the eastern Beringian endemic *Microtus miurus* Osgood is also specifically distinct (i.e. *Paranoplocephala batzlii* Haukisalmi, Henttonen & Hardman, 2006; see Haukisalmi et al. 2006).

The present molecular phylogenetic analysis shows unequivocally that the *P. omphalodes*-like cestodes in Buryatia do not represent the true *P. omphalodes* (Fig. 1).

The Buryatian specimens form a monophyletic group that is sister to the divergent North Alaskan subclade of *P. jarrelli*. The topology and high statistical support of the tree suggests that these two clades are both independent species, forming a sister group for the true, Holarctic *P. jarrelli*.

In the present material, the Buryatian *P.* cf. *omphalodes* occurred exclusively in *Microtus fortis* and *M. oeconomus*. *Paranoplocephala omphalodes* has earlier been reported from *M. maximowiczii*, *M. oeconomus*, *Myodes rufocanus* and *Apodemus peninsulae* in Buryatia and adjacent regions (Machul'skii 1958; Zhaltsanova 1992). The earlier Buryatian records of *P. omphalodes* from *Myodes rufocanus* probably represent another, recently described species (i.e. *Paranoplocephala buryatiensis* Haukisalmi, Hardman, Hardman, Laakkonen, Niemimaa & Henttonen, 2006; see below).

Paranoplocephala cf. *omphalodes* from Buryatia may be primarily associated with the Asian *Microtus* species, i.e. *M. fortis* and *M. maximowiczii*, because it is not known from *M. oeconomus* outside Buryatia. *Paranoplocephala* cf. *omphalodes* will be later described as a new species.

Paranoplocephala cf. *omphalodes* was present in seven of the 12 study sites, highest prevalences being 20-23% (Table 1).

Voucher specimen: MSB Endo 153 from *M. oeconomus* (Nizhnaya Ivolga).

Paranoplocephala blanchardi (Moniez, 1891)

Paranoplocephala blanchardi (Moniez, 1891) *sensu* Tenora et al. (1985b) is primarily a parasite of *Microtus* spp. in Europe (Haukisalmi et al. 1994; Tenora et al. 1985b) and western Siberia, extending at least to the Novosibirsk region in the east (Chechulin 1998). The conspecificity of two Buryatian specimens of *P. blanchardi* (from *Microtus fortis*) with the European specimens is confirmed by the present molecular phylogenetic analysis (Fig. 2). The Buryatian records thus represent the easternmost finding of this species. Despite considerable sampling effort, *P. blanchardi* has not been found in north-eastern Siberia (Magadan region, Chukotka; unpublished BCP records).

P. blanchardi was found at a single study site (prevalence 17%) (Table 1).

Voucher specimen: MSB 154 from *M. fortis* (Maloje Kolesova).

Paranoplocephala feodorovi (Gulyaev & Chechulin, 1996)

Paranoplocephala feodorovi was originally described as *Parandrya feodorovi* Gulyaev & Chechulin, 1996 from *Arvicola terrestris* (L.) (primary host), *Microtus agrestis* and *M. maximowiczii* from the Novosibirsk region in the south of West Siberia (type locality) and Zabaikalsk in Buryatia (Gulyaev and Chechulin 1996; see Chechulin 1998 for further records in the latter region). Only a single specimen from *Microtus fortis* conforming to the description of *P. feodorovi* was encountered during the present study, which supports the secondary role of *Microtus* spp. in the epidemiology of this cestode.

Morphologically, *P. feodorovi* is closely related to *P. blanchardi*, the main difference being the antiporal extent of the testes (extending across the antiporal ventral longitudinal osmoregulatory canal in *P. blanchardi*, but not in *P. feodorovi*). However, *P. feodorovi* is not genetically related to *P. blanchardi*. In the COI phylogram, *P. feodorovi* was associated with *P. oeconomi*, appearing as one of the basal lineages within *Paranoplocephala* (Fig. 2). The phylogenetic position of *P. feodorovi* supports the hypothesis that *Parandrya* Gulyaev & Chechulin, 1996 is a synonym of *Paranoplocephala s.l.*, as suggested by Haukisalmi and Henttonen (2000) and Haukisalmi and Wickström (2005).

Voucher specimen: MSB Endo 155 from *M. fortis* (Maloje Kolesova).

Paranoplocephala buryatiensis Haukisalmi, Hardman, Hardman, Laakkonen, Niemimaa & Henttonen, 2006

P. buryatiensis, described from Buryatian material, is primarily a parasite of *Myodes rufocanus* (Haukisalmi et al. 2007a), although it was found occasionally in *Microtus fortis* in the present material. Its known range spans from Buryatia to north-eastern Siberia. However, it does not occur in the westernmost populations of *Myodes rufocanus* in northern Fennoscandia (Haukisalmi et al. 2007a).

P. buryatiensis is morphologically and genetically closely related to *P. longivaginata* Chechulin & Gulyaev, 1998 from *Myodes rutilus* (below); they form a strongly supported clade in the mtDNA phylogenies (Fig. 2 and Haukisalmi et al. 2007a). Haukisalmi et al. (2007a) provided evidence for phylogenetic codivergence of *P. buryatiensis* and *P. longivaginata* with their primary hosts.

P. buryatiensis occurred in *Myodes rufocanus* at four of the eight study sites, the prevalence in Pasolskaya (43%) being higher than in the other sites (0-10%). It also occurred in *Microtus fortis* at two study sites, where it also parasitized the primary host *Myodes rufocanus*.

Type specimen: USNPC 97137 from *Myodes rufocanus* (Pasolskaya); paratype specimen: USNPC 97138 from *M. rufocanus* (Pasolskaya); voucher specimen: US-NPC 97139 from *Microtus fortis* (Kamensk).

Paranoplocephala longivaginata Chechulin & Gulyaev, 1998

P. longivaginata was described from *Myodes rutilus* and, secondarily, from *Sciurus vulgaris* L., in Buryatia and the neighbouring Amurskaya Oblast (Chechulin and Gulyaev 1998). In addition to Buryatia and adjacent regions, it has been found from *Myodes rutilus* in north-eastern Siberia (Magadan region; Haukisalmi et al. 2007a). However, *P. longivaginata* does not occur in *M. rutilus* in north-western North America (unpublished BCP data).

P. longivaginata occurred at five of the seven study sites, but always at a low prevalence.

Voucher specimen: MSB Endo 156 from *Myodes rutilus* (Verhnaya Berezovka).

Catenotaeniidae

Catenotaenia sp. 1

The specimens from *Cricetulus barabensis* resemble *Catenotaenia dendritica* (Goeze, 1782), *C. laguri* Smith, 1954, *C. linsdalei* McIntosh, 1941, *C. reggiae* Rausch, 1951 and *C. ris* Yamaguti, 1942 in having numerous uterine branches (39-43 in the present specimens). However, these species have either significantly more numerous (*C. den-*

dritica, C. reggiae, C. ris) or less numerous (*C. laguri, C. linsdalei*) testes than the present specimens (ca. 80). Moreover, three of these species are specific parasites of sciurids (*C. dendritica, C. reggiae, C. ris*), two other have been found only from *Lemmiscus* Thomas (*C. laguri*) and *Thomomys* Wied-Neuwied (*C. linsdalei*), and three of them are known only from North America (*C. reggiae, C. laguri, C. linsdalei*). We conclude that the present specimens from *C. barabensis* represent an undescribed species of *Catenotaenia* Janicki, 1904.

Zhaltsanova (1992) reported *Catenotaenia cricetorum* Kirshenblat, 1949 from *C. barabensis* from Buryatia, but did not provide any morphological data for the cestode. We assume that the specimens of Zhaltsanova (1992) from *C. barabensis* actually represent the same undescribed species as found by us from Buryatian hamsters.

Voucher specimen: MSB Endo 157 from *C. barabensis* (Ganzurinov).

Catenotaenia sp. 2

The cestodes from *Apodemus peninsulae* had 29-34 uterine branches, which corresponds with *Catenotaenia afghana* Tenora, 1977, *C. californica* Dowell, 1953, *C. neotomae* Babero & Cattan, 1983 and *C. peromysci* Smith, 1954. However, the cestodes found by us have a clearly divided testicular field, a feature which occurs in *C. californica* but not in the three other species mentioned above. Compared with the present material, *C. californica* has markedly wider body (0.75-0.83 mm in the present specimens) and smaller scolex (ca. 0.38 mm in the present specimens). Since *C. californica, C. neotomae* and *C. peromysci* are Nearctic parasites of heteromyid and sigmodontid (Neotominae) rodents, it is unlikely that they would occur in a murid rodent in Eurasia. The brief original description of *C. afghana* was based on material from two unrelated host species, *Cricetulus migratorius* (Pallas) and *Alticola* sp. from Afghanistan, and it was not stated which was the type host. Moreover, no type specimen was designated (Tenora 1977). Ganzorig et al. (1999) later redescribed *C. afghana* from *Lasiopodomys brandtii* (Radde) from Mongolia but it is probable that the specimens assigned to *C. afghana* include more than one species. The specimens from Buryatian *A. peninsulae* may therefore represent another undescribed species of *Catenotaenia*.

Voucher specimen: MSB Endo 158 from *A. peninsulae* (Kamensk).

Hymenolepididae

Arostrilepis horrida (von Linstow, 1901) *s.l.*

In the present material, *Arostrilepis horrida*-like cestodes occurred commonly in all *Microtus* and *Myodes* species and accidentally in *C. barabensis* but were absent in *A. peninsulae*. The data of Zhaltsanova (1992) show an equally wide host spectrum

for *Arostrilepis horrida*-like cestodes in Buryatia. Three species have been described within the *A. horrida*-complex, i.e. *A. horrida* from an unknown rodent host, *A. beringiensis* Kontrimavichus & Smirnova, 1991 from *Lemmus sibiricus* and *A. microtis* Gulyaev & Chechulin, 1997 from *Microtus* spp. (see Kontrimavichus and Smirnova 1991 and Gulyaev and Chechulin 1997). However, applying molecular methods, the BCP has demonstrated a complex of at least 10 species of *A. horrida*-like cestodes that are poorly differentiated morphologically (Cook et al. 2005, and K. Galbreath and E. P. Hoberg, unpublished). For example, there may be five *Arostrilepis*-species in *Myodes* spp. (species previously assigned to *Clethrionomys*) and two species in *Microtus* spp. in the Holarctic region. The situation is complicated by the fact that it is not known which one (if any) of them is the true *A. horrida*. Therefore, it is not possible to assign the present specimens to a particular species of *Arostrilepis*. However, it is probable that the Buryatian material includes at least one undescribed species, i.e. that/those occurring in *Myodes* spp.

Voucher specimens: MSB Endo 159 from *Microtus fortis* (Kamensk), MSB Endo 160 from *M. oeconomus* (Nizhnaya Ivolga), MSB Endo 161 from *Myodes rufocanus* (Kamensk), MSB Endo 162 from *Myodes rutilus* (Muhorshibir).

Rodentolepis sp.

Rodentolepis sp. from *Cricetulus barabensis* was characterized by 22-24 fraternoid hooks. In this respect it resembles *Rodentolepis fraterna* (Stiles, 1906) (see Genov 1984) and *R. sinensis* (Oldham, 1929) (see Ryzhikov et al. 1978), although the hooks of the present species are somewhat longer (0.020-0.032 mm) than those of *R. fraterna*. In addition, the scolex of the present cestode is significantly larger (0.24-0.26 mm) than that of *R. sinensis*, and its eggs are significantly longer (0.060-0.075 mm) than those of *R. fraterna*. It is probable that *Rodentolepis* sp. from Buryatia represents an undescribed, host-specific species of *C. barabensis*. The high variation in hook length suggests that the material may include more than one species.

Zhaltsanova (1992) reported *R. straminea* (Goeze, 1782) from *C. barabensis* and *Myodes rufocanus* from Buryatia, but that identification is dubious, because many forms, including *R. fraterna* and *R. nana* (Siebold, 1852), have been synonymized with *R. straminea* in the Soviet/Russian literature (see Ryzhikov et al. 1978).

Voucher specimen: MSB Endo 163 from *C. barabensis* (Sharaldai).

Diversity and distribution

The present study shows that there are at least 11 species of cestodes in the Buryatian rodents (assuming 2 species in the *A. horrida*-complex), of which at least five species are previously unreported from the region. The anoplocephalid cestode fauna of Buryatian arvicoline rodents (voles and lemmings) includes a minimum of seven species

(Table 2). The species diversity of the corresponding fauna is equally low in North-East Siberia (six species), whereas the European fauna consists of at least 17 species. Additionally, almost half (eight species) of European anoplocephalid species are endemic

Table 2. Host and geographic distribution of anoplocephalid cestodes of voles and lemmings in Europe, Buryatia and North-East Siberia. The host species are: *Myopus schisticolor (sch)*, *Ondatra zibethicus (zib)*, *Arvicola amphibius (amb)*, *Chionomys nivalis (niv)*, *Microtus agrestis (agr)*, *M. arvalis (arv)*, *M. cabrerae (cab)*, *M. fortis (for)*, *M. guentheri (gue)*, *M. oeconomus (oec)*, *M. subterraneus (sub)*, *Myodes glareolus (gla)*, *My. rufocanus (rufo)* and *My. rutilus (ruti)*. The Arctic lemmings of the genera *Lemmus* and *Dicrostonyx* have been excluded, because they are absent in Buryatia. The primary host species in each region (when evident) have been in indicated in bold.

	Europe	**Buryatia**	**North-East Siberia**	**General distibution**	**Sources**
Anoplocephaloides dentata	**niv**, *arv*	-	-	Europe	1, 2, 3
A. cf. *dentata*	**oec**	**for**; *rufo*	**oec**	Holarctic	1, 2, 3
A. cf. *dentata* 2	*agr, oec*	-	-	Europe	1, 2, 3
A. cf. *dentata* 3	**arv**	-	-	Europe	1, 2, 3
Anoplocephaloides mascomai	**cab**	-	-	Europe	4
Microcephaloides sp. 1	*agr, oec*	-	-	Europe	2
Microcephaloides sp. 2	**gue**		-	Europe	2
Microcephaloides sp. 3	-	-	**oec**	Holarctic?	2
M. tenoramuraiae	*niv, sub*	-	-	Europe	5
Paranoplocephala aquatica	**amb**, *zib*	-	-	Europe	6
P. blanchardi	**agr, arv**, *oec; gla*	**for**	-	Palearctic	7, 8
P. buryatiensis	-	**rufo**; *for*	**rufo**	Palearctic	8, 9
P. feodorovi	-	**amb**; *for*	-	Palearctic	8, 10
P. gubanovi	-	**sch**	-	Palearctic	20
P. gracilis	**agr**, *arv, oec; gla, rufo, ruti*	-	-	Palearctic	7, 8, 11
P. janickii	**arv**	-	-	Palearctic	7
P. jarrelli	**oec**	-	**oec**	Holarctic	8, 12, 13
P. kalelai	**rufo**, *gla*	-	-	Palearctic	14 , 15
P. longivaginata	-	**ruti**	**ruti**	Palearctic	8, 9, 16
P. oeconomi	**oec**	-	-	Palearctic	17
P. omphalodes	**arv, agr**; *gla*	-	-	Palearctic	12, 14
P. cf. *omphalodes*	-	*for, oec*	-	Palearctic	8
P. primordialis (s.l.)	-	-	*ruti; oec*	Holarctic	18
P. yoccozi	**niv**	-	-	Palearctic	19

1, Wickström et al. 2005. 2, Haukisalmi et al. 2008. 3, L.M. Hardman et al., unpublished. 4, Murai et al. 1980. 5, Genov and Georgiev 1988. 6, Genov et al. 1996. 7, Tenora et al. 1985b. 8, present study. 9, Haukisalmi et al. 2007a. 10, Gulyaev and Chechulin 1996. 11, Tenora and Murai 1980. 12, Haukisalmi et al. 2004. 13, Haukisalmi et al. 2006. 14, Tenora et al. 1985a. 15, Haukisalmi et al. 2007b. 16, Chechulin and Gulyaev 1998. 17, Gubányi and Murai 2002. 18, V. Haukisalmi and R. L. Rausch, unpublished. 19, Haukisalmi and Henttonen 2005. 20, Gulyaev and Krivopalov 2003.

to this region. Anoplocephalid cestodes of Buryatian rodents consist predominantly of Palaearctic species; only two of them may be endemic to Buryatia or Central Eurasia. Endemism is equally low in North-East Siberia. It should be noted that one of the most specious anoplocephalid lineages of arvicoline rodents, *Microcephaloides* spp. (earlier known as *Anoplocephaloides variabilis*-like cestodes), appears to be absent in Buryatia, although it occurs widely in Europe and North America, and sporadically in North-East Siberia (Haukisalmi et al. 2008).

The high species diversity and endemism in Europe is partly due to the high taxonomic diversity of voles in that region; of the 14 vole and lemming species considered in the present comparison, seven occur exclusively in Europe or western Eurasia. If we restrict the comparison to the vole species with a wide Palaearctic or Holarctic distribution (*Microtus oeconomus*, *Myodes rufocanus* and *M. rutilus*), Europe (eight spp.) still shows somewhat higher species diversity than Buryatia (four species) and North-East Siberia (six spp.). The differences in species diversity may also reflect the more extensive research and use of molecular methods for the European fauna. However, high European species diversity has also been indicated for anoplocephalid cestodes of lagomorphs (Spasskii 1951), suggesting that this phenomenon may have a more general biogeographical and/or historical explanation. The existing phylogenetic data indicate a possible European origin for *Microcephaloides* Haukisalmi, Hardman, Hardman, Rausch & Henttonen, 2008 (see Haukisalmi et al. 2008) and *Paranoplocephala s. str.* (see Haukisalmi et al. 2004), suggesting that Europe may have acted as a centre of origin for several independent anoplocephalid lineages. However, the phylogenetic relationships among various anoplocephalid lineages are still unresolved, which impedes more comprehensive analyses on the historical biogeography of anoplocephalid cestodes of arvicoline rodents.

The faunistic connections of Buryatia seem to be slightly closer to North-East Siberia than to Europe; Buryatian anoplocephalids shared three and two species with these regions, respectively. Moreover, an unexpected connection is seen between Buryatia and eastern Beringia; namely, the sister clade/species of the Buryatian *P.* cf. *omphalodes* occurs in the northernmost Alaska, but probably not elsewhere in North America. Neither clade has been found in extensive studies in the North-East Siberia (BCP), suggesting that the present distribution represents a relict of an earlier continuous distribution. On the continental level, the Buryatian taiga corridor has probably not played a significant role as a migration pathway among anoplocephalid cestodes of rodents; only one species with a continent-wide distribution (*A.* cf. *dentata*) occurred in Buryatia. Moreover, *A.* cf. *dentata* also occurs also in North-Central Siberia (Tunguska river region; Haukisalmi et al. 2009) and may not necessarily have utilized the Buryatian corridor.

The present and earlier studies (Haukisalmi et al. 2008, Haukisalmi et al. 2004, Hu et al. 2005) show that molecular markers, such COI sequences, are necessary tools in the taxonomy of anoplocephalid cestodes, which lack a rostellum and hooks and which can be devoid of reliable distinguishing features. It can be estimated that 50-60% of species diversity of anoplocephalid cestodes of voles and lemmings in the

Holarctic region would have remained undetected if the taxonomy had been based on morphological features only (Table 2 and unpublished records of the BCP and present authors). No molecular systematic studies exist for catenotaeniids but because they also lack anchoring devices, additional, cryptic species diversity is expected to occur also within this family.

The present results demonstrate high variation among study sites in cestodes of Buryatian rodents, with the exception of the ubiquitous *A. horrida*-complex (Table 1). Haukisalmi and Henttonen (1999) showed that patchiness is a predictable feature of certain helminths of rodents and that such patches may be remarkably persistent. The BCP studies also reveal fine-scaled spatial variation in many anoplocephalid cestodes of voles and lemmings in Alaska and adjacent regions (Haukisalmi et al. 2009, Haukisalmi et al. 2004, Wickström et al. 2003). Patchiness has an obvious implication for assessment of the biodiversity cestodes: species and genetic diversity may be much underestimated in samples that are not spatially comprehensive. In addition, helminths may be very specialized in a certain cohort(s) and/or sex of the host, related to seasonally changing heterogeneity of rodent populations (Haukisalmi et al. 1995), which should also be considered in the estimation of parasite diversity.

Acknowledgements

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